The Genus *Dolichovespula* and an Addition to Its Known Species of North America

(Hymenoptera:Vespidae)

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The generic and subgeneric divisions of the subfamily Vespinae were described by Bequaert (1930, 1931). He concluded that the subfamily included three genera; *Provespa* Ashmead for the Oriental nocturnal hornets, *Vespa* Linnaeus for the true hornets, and *Vespula* Thompson for the yellowjackets. He recognized two subgenera of *Vespula; Vespula* for species with short oculo-malar spaces, and *Dolichovespula* Rohwer for species with long oculo-malar spaces.

The most recent major work on the taxonomy and distribution of the Nearctic Vespini was that of Miller (1961) who accepted the generic concepts of Bequaert. By means of distributional data and by accepting "stable color patterns as supplementary evidence to define species" he was very successful in clarifying the status of most North American species. He was also correct when he stated that further elucidation of the taxonomy of the yellowjackets would have to come from field studies (Miller 1958).

In recent years many workers have published biological and behavioral studies of these wasps and most of Miller's taxonomic conclusions have been substantiated. These studies have also provided increasing evidence to support the validity of generic status for *Dolichovespula* as suggested by Guiglia (1948) and subsequently accepted by Bluthgen (1961), Yamane (1975), and Greene et al. (1976). Of the numerous classifications of Vespinae proposed during the past 50 years, that of Guiglia is the most natural in the opinion of the author and it is followed in this paper.

Generic characters.

A comparison of the following characters serves to define the genera *Vespula* and *Dolichovespula* as natural taxonomic groups at least as distinct from one another as from the closest relative, *Vespa*.

Vespula Thomson, 1869. Opusc. Ent. v. 1 p. 79.

Type: *Vespa austriaca* Panzer. Designated by Ashmead, 1902.

(a) oculo-malar space at most half the length of the penultimate antennal segment
(b) lateral, vertical carina on pronotum obsolete or faintly marked in only the lower portion
(c) branches of the penis completely fused resulting in a disc-like or saddle-shaped apical lobe
(d) tyloides (welts) not present on apical flagellar segments of the male antennae
(e) mandible of last-instar larva always tridentate
(f) spiracular atria of last-instar larva armed with simple, mostly unbranched spines.

The Pan-Pacific Entomologist 54:131-142. April 1978.

Dolichovespula Rohwer, 1916. Conn. State Geol. and Nat. Hist. Survey Bull. 22:642.

Type: *Vespa maculata* Linnaeus

(a) oculo-malar space nearly as long or longer than the penultimate antennal segment
(b) lateral, vertical carina on pronotum well developed in the upper portion
(c) branches of the penis incompletely fused resulting in a pair of pointed apical lobes
(d) tyloides (welts) usually present on the apical flagellar segments of the male antennae
(e) mandible of last-instar larva always terminating in a single ventral apical tooth[1]
(f) spiracular atria of last-instar larva armed with many multibranched spines

The author has collected and examined adults of all known North American species of both genera and found the first three characters to be consistent. The only exception to the fourth, the presence of tyloides on the male antennal segments, in North American *Dolichovespula* species is the social parasite, *Dolichovespula artica* Rohwer. The larval characters are consistent in all North American species collected. Only the larvae of *Vespula intermedia* (Buysson) and *V. austriaca,* the nests of which have not yet been discovered in North America, have not been examined.[2]

In the course of field investigations of the North American yellowjackets, the author has discovered that *Dolichovespula saxonica* (Fabricius) which has been considered to be Palearctic is also widely distributed in the Nearctic fauna (Fig. 2). A definitive character for discrimination of this species from related Nearctic species is established and included in the key to species at the end of this paper.

Although it was possible to define the distribution of *D. saxonica* in North America reasonably well, available knowledge on the distribution of this and other *Dolichovespula* species in the Palearctic and Oriental regions was found to be incomplete. Any continuity between the Nearctic and Palearctic populations must, therefore, remain hypothetical.

The Subgenera of Dolichovespula

Within North America, only two subgenera of *Dolichovespula* as defined by Bluthgen (1943) are present. The subgenus *Dolichovespula* (S. Str.) is represented by the baldfaced "hornet", *D. maculata*, which is a particularly distinct, widespread species. It is mentioned here only to provide additional distributional information. Miller (1961) pre-

[1]The reported exception to this larval mandible configuration was that of *Dolichovespula silvestris* Scopoli which according to Short (1952) had a tridentate mandible. I have examined larvae of *D. silvestris* collected by M.E. Archer and provided to me by O.W. Richards of the British Museum. The larval mandible is not tridentate but is typical of the genus terminating in a single emarginate ventral apical tooth. As Prof. Richards states "the mandibles of the larvae of *Dolichovespula* are all very much alike" (pers. com.).

[2]Report of the parasitic association of *V. austriaca* and *Vespula maculifrons* (Buysson) by Evans (1975) was erroneous (pers. com.). The host relationship for *V. austriaca* in North America has yet to be established. Field observations and collection data indicate that *Vespula acadica* (Sladen) has the greatest distributional correlation with *V. austriaca* and may well be the usual host of this parasitic species. It is probable that *V. austriaca* may parasitize other Nearctic species of the subgenus *Allovespula* as well.

sented distributional data which was quite complete, but he did not report the occurrence of this species in Alaska. The author collected several workers of *D. maculata* between Fairbanks and Harding Lake, about 48 km to the southeast, in early August of 1973 and 1976. It was not encountered at other collecting sites in Alaska during these years.

The remaining North American *Dolichovespula* are found in the subgenus *Boreovespula*. This taxon is particularly homogeneous and has historically presented taxonomic difficulties at the species level. Birula (1930) recognized only one Palearctic species, *Dolichovespula norwegica* (Fabricius) and he considered *D. saxonica* to be a subspecies even though he recognized structural differences in the shape of the ocellar triangle, the pattern in punctation, and the male genitalia. These differences were subsequently used to separate the two species by European taxonomists (e.g. Bluthgen 1961, Guiglia 1948).

It was only where series of specimens were strikingly different in appearance that Birula saw fit to distinguish them by a subspecific name. Such a case was that of *Dolichovespula pacifica* (Birula) which he considered to be another subspecies of *D. norwegica*. In his revision of the Oriental *Boreovespula,* Yamane (1975) found that there were actually at least two species which had been included in collections under the name of *D. pacifica*. Ratios between the measurements of head-width versus oculo-malar length of field-collected specimens yielded two distinct groups. When worker specimens collected from nests were measured, he found that their mean ratios agreed with one of the mean ratios previously established. Using these data and other characters (ocellar placement and clypeal markings), he was able to separate the specimens into *D. pacifica* and *Dolichovespula saxonica nipponica* Yamane. Judging from Birula's description of some males of *D. pacifica* which had no antennal tyloides, he may also have been examining male specimens of a parasitic species. Both *D. pacifica* and *D. s. nipponica* possess tyloides on their antennal flagella and I have been provided male specimens under the name *Dolichovespula adulterina* (Buysson) by Mr. Yamane which are colored much like *D. pacifica* but lack tyloides.

Birula also commented at length with regard to the apparent transition in coloration of the markings on *D. norwegica* from yellow to ivory-white as he followed the distribution of this species from Europe towards East Siberia. He considered the whitish marked forms to be transitional to *D. pacifica* even though typically yellow marked *D. norwegica* were often recorded from the same localities. I have only seen two queen specimens of this white marked form, both from the island of Sakhalin. These specimens kindly loaned to me by Mr. Yamane and identified as *D. norwegica* subsp., are very similar to the Nearctic species *Dolichovespula albida* (Sladen) (= *Vespa marginata*

Kirby preocc) but without examing workers and males, their relationship is unsure. It would certainly not be inconceivable that the distribution of *D. albida* could, in fact, be Holarctic and that within East Siberia it could be sympatric with typical *D. norwegica* thus explaining Birula's observations of the presence of both color forms.

While studying *Dolichovespula* in Alaska during the summer of 1973, the author found what first appeared to be atypical colonies of *Dolichovespula norvegicoides* (Sladen). Typical nests of that species which I have collected, were invariably built in cavities in stream banks or within root tangles of uprooted trees adjacent to streams. They were nearly spherical and about 6 cm in diameter with the outer envelopes of grey fibrous paper, entire from the nest pole to its ventral entry. This description also fits nests of *D. norvegicoides* reported by previous investigators. One atypical nest was located inside a wall void of a wood-siding covered building at King's Mountain Wayside, Alaska, about 160 km southeast of Anchorage. The nest was not visible through the 2 cm gap in the siding which was being used by the workers as an entrance. Worker activity was at a rate of about ten per minute. They were net collected until activity had nearly ceased. The siding was then removed, exposing a nest of about 13 cm diameter with a thickness of 4.1 cm due to the constraints of the void (Fig. 1). The colony contained the queen mother and 55 workers, including those which had been netted. It also contained a queen of the social parasite *D. arctica*. Emergence of male specimens of *D. arctica* from nest combs within the next few days indicated that a *D. arctica* queen had been present in the nest for at least three weeks before the nest was collected. The nest envelope differed from *D. norvegicoides* nests in that it was composed of nine concentric sheets of grey paper only the middle three of which reached the nest entrance. The outer three sheets each terminated closer to the nest attachment than the one immediately inside it giving the nest a tiered appearance similar to the nests of Palearctic *D. saxonica*.

A second nest of this species was found in a supraterrestrial nest site at Eagle River, Alaska. The nest, which was 10.7 cm in diameter and had one worker and one queen comb, had been constructed on the surface of the ground in a shallow cavity hollowed out of leaf litter among shrubs about 15 meters from the edge of the river. As the term "supraterrestrial" is also meant to indicate, the wasps did not appear to have excavated soil for the nest site. The collected nest compliment included 41 workers, no identifiable queen mother, 11 new queens and 26 males. The combs were held for further emergence and subsequently produced 51 more queens and four males. The nest envelope was of grey fibrous paper and incorporated leaf fragments. Individual sheets were interconnected at many points, resulting in a spongy fibrous mass rather than the discrete sheets of an aerial or cavity nest.

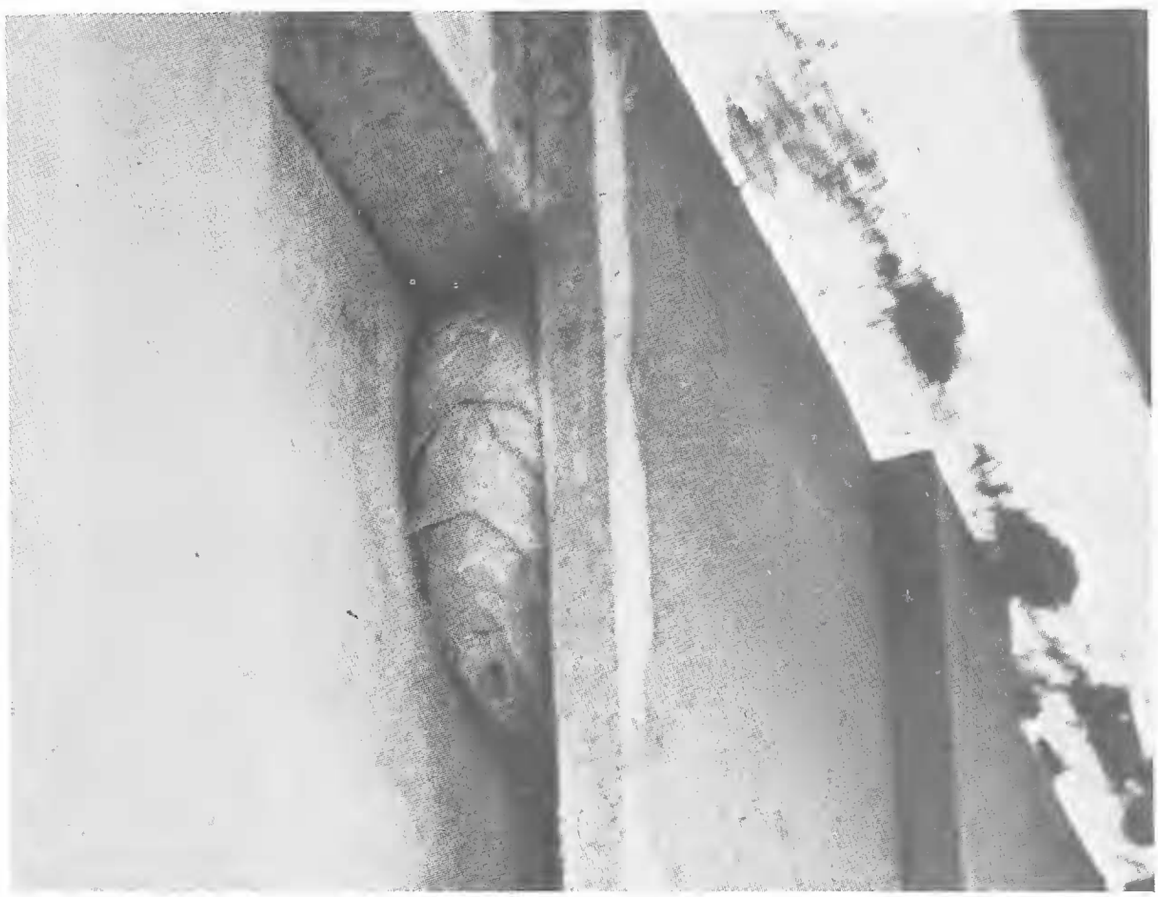

Figure 1. A nest of *Dolichovespula saxonica* (F.) in situ in a building wall void at King's Mountain, Alaska. Siding had been removed to expose the nest.

Methods and Materials

Since the oculo-malar space is a useful character separating *Vespula* and *Dolichovespula*, and is shown to be applicable at the specific level (Yamane 1975), the constancy of this character was investigated in North American *Boreovespula*. The most widespread and easily recognizable species in the Nearctic region is *Dolichovespula arenaria* (Fabricius). This species is very common and specimens were available from many localities throughout its distributional range. A series of worker specimens was examined from each of 17 widely separated localities. The width of the head at its widest point and the length of the oculo-malar space were measured for each specimen. The ratio between these measurements for each specimen and the mean ratio for each series were calculated.

Six series of worker specimens of *D. norvegicoides* from various localities as well as samples from the two previously described Alaskan nests, a sample netted at Eagle River, Alaska and a sample from Banff, Alberta, Canada, were measured and ratios calculated. The combined data from the 27 groups which had been measured were subjected to analysis of variance and Duncan's Multiple Range Test. In order to show possible clinality of the oculo-malar/head width

ratios as correlated to latitude, longitude and elevation of the sites of collection, a stepwise regression analysis was performed on each of the three sample groups defined by the previous tests.

Results

In summary of the analytical results presented in Table 1, the head width/oculo-malar ratios of all 17 *D. arenaria* samples were significantly different from those of the six samples of *D. norvegicoides*. The remaining four samples of wasps were also significantly different from *D. norvegicoides* which they closely resembled, but were not different from *D. arenaria* in head width/oculo-malar ratios. Results of the stepwise regression analysis of the 17 *D. arenaria* samples

Species	n	$\bar{x}$ HW (mm)	$\bar{x}$ OM (mm)	HW/OM $\bar{x}$ (SD)[a]	Specimen origin		
					Latitude	Longitude	Elevation (M)
D. arenaria	5	3.30	0.45	7.258 (0.315)a	34°10'	117°05'	1830
	10	3.26	0.45	7.222 (0.360)a-b	35°30'	83°00'	915
	10	3.46	0.48	7.172 (0.230)a-c	37°55'	122°40'	300
	10	3.38	0.47	7.154 (0.255)a-c	37°45'	119°30'	3200
	8	3.36	0.47	7.141 (0.375)a-c	48°30'	96°40'	300
	7	3.52	0.49	7.116 (0.111)a-d	37°45'	122°26'	150
	5	3.45	0.49	7.052 (0.382)a-e	37°20'	122°25'	230
	10	3.29	0.47	7.030 (0.216)a-f	48°07'	123°30'	150
	7	3.55	0.51	7.027 (0.395)a-f	36°30'	118°40'	1830
	10	3.30	0.48	6.878 (0.357)c-g	64°25'	146°50'	275
	10	3.32	0.49	6.872 (0.304)c-g	64°25'	146°52'	230
	10	3.45	0.51	6.764 (0.160)e-h	42°20'	85°15'	230
	8	3.41	0.51	6.740 (0.283)f-h	55°00'	119°00'	610
	10	3.32	0.49	6.737 (0.264)f-h	40°48'	72°42'	75
	10	3.47	0.52	6.709 (0.187)g-h	53°28'	114°10'	640
	6	3.50	0.53	6.653 (0.184)g-h	58°40'	136°40'	30
	10	3.53	0.54	6.572 (0.283)h	61°20'	149°30'	120
D. norvegicoides	10	3.14	0.54	5.877 (0.242)i	64°25'	146°25'	230
	10	3.20	0.55	5.862 (0.287)i	49°47'	94°29'	305
	10	3.38	0.58	5.845 (0.192)i	53°28'	114°00'	640
	8	3.21	0.56	5.730 (0.343)i	45°34'	69°35'	460
	10	3.08	0.54	5.730 (0.317)i	44°23'	64°15'	75
	10	3.04	0.54	5.609 (0.198)i	64°25'	146°55'	230
D. saxonica	10	3.13	0.44	7.068 (0.386)a-e	51°30'	116°00'	2440
	10	3.23	0.47	6.961 (0.266)b-g	61°46'	148°30'	245
	10	3.27	0.48	6.815 (0.295)d-h	61°20'	149°30'	120
	10	3.25	0.48	6.815 (0.289)d-h	61°20'	149°30'	120

[a]Mean ratios not followed by the same letter are significantly different ($P = < .05$) according to Duncan's Multiple Range Test.

Table 1. Head width/Oculo-malar (HW/OM) length ratios of some Nearctic *Dolichovespula* species and correlation to the locations of the sites of specimen collections.

indicate that latitude is the factor most strongly correlated with head width/oculo-malar ratio, followed by longitude and elevation. The formula generated by the analysis was, ratio = 7.3818 - 0.01728 (degrees latitude) + 0.003 (degrees longitude) + 0.00003 (meters elevation). r = 0.4656 n = 146.

With *D. norvegicoides* no significant correlation could be shown among the factors analyzed but this may be due to smaller sample size. Analysis of the four samples of the remaining *Dolichovespula* species again showed a stronger correlation of the ratio with latitude than with longitude or elevation. The formula generated for this species was, ratio =−1.77769 + 0.13872 (degrees latitude) + 0.99968 (meters elevation). r = 0.3390 n = 40. Due to the narrow range of longitudes represented in the samples, no longitude correlation was calculable.

The data presented in Table 1 show that there is a clinality with regard to the head width/oculo-malar length ratio. This ratio becomes smaller with increasing latitude and elevation. The influence of elevation would appear to be very slight from the formulae generated by stepwise regression analysis.

Discussion

The analytical tests performed on data from worker specimens proved the reliability of head measurements for the separation of two very similar appearing species. Examination of queens and males was made to assure that they could also be properly determined. Sixty-one queen specimens which had been previously assigned to *D. norvegicoides* were measured and their oculo-malar/head width ratios calculated. As had been found with the worker specimens, the queens also exhibited two modes with regard to this ratio. The geographic distribution of queens and workers with each type of oculo-malar space coincided.

In order to assure the assignment of each of the species to the proper taxon, the type specimen of *D. norvegicoides* was obtained from the Canadian National Museum. The lectotype queen (No. 6823, Amherst, Nova Scotia, VII-2-15) was found to possess the longer oculo-malar space of 0.77 mm and a head width of 3.80 mm for a ratio of 5.28. Examination of the allotype male (Sladen's No. 2186, Inverness, B.C., July 1910, J.H. Keen collector) was also made. This locality is just to the SSE of Prince Rupert, B.C., and is within the geographic distribution of *D. norvegicoides* as delimited by the queens and workers.

Although the digitus of the male genitalia provides an excellent means of separating some vespine species within the *Boreovespula*, the male genitalia of other species are almost identical and other characters must be used to separate these species. Within the subgenus *Boreovespula* it has been recognized that the presence or

absence of tyloides or welts on the apical flagellar segments of the male antennae is characteristic of species. For example, Bequaert (1931) was able to structurally separate males of *D. albida* which possess one basal tyloide on each of the last five antennal segments from those of *D. norvegicoides* which possess two tyloides on each of the last six segments. Examination of the allotype male verified this tyloide arrangement as did other males collected within the geographical distribution of *D. norvegicoides* as shown on Figure 2.

Males collected from the mountains of the Continental Divide of North America, where the species with the short oculo-malar space is distributed, possess a tyloide arrangement different from either *D. norvegicoides* or *D. albida*. They possess a single basal tyloid on the apical segment, two tyloides on the next three segments and a single basal tyloide on the fifth and sixth segments. The author has designated this arrangement as a tyloide formula of 1-2-2-2-1-1. This

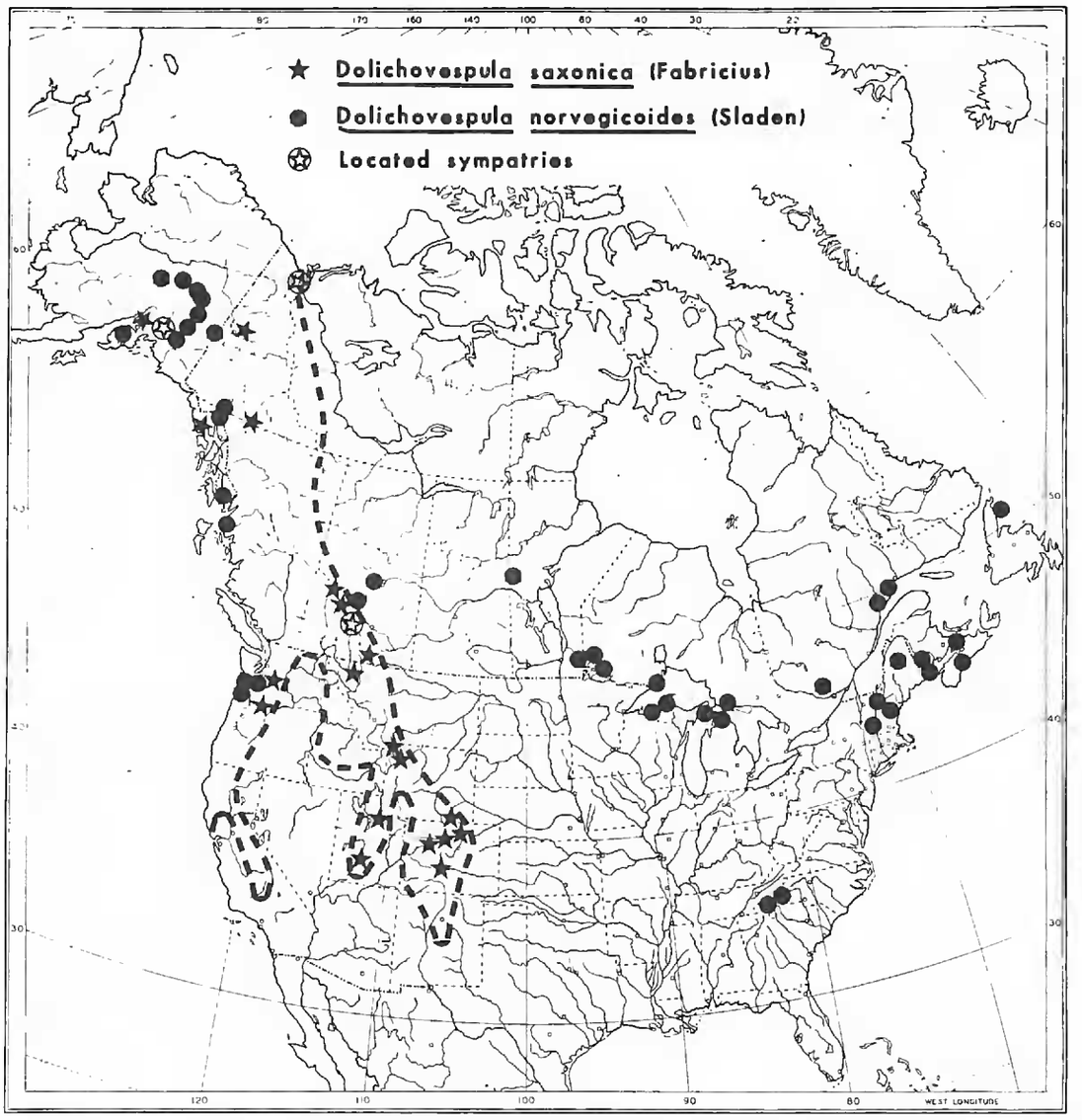

Figure 2. The distribution of *Dolichovespula saxonica* (F.) and *Dolichovespula norvegicoides* (Sladen) in North America. Note the dotted line which roughly outlines the major mountainous areas of the west.

formula exactly duplicates the tyloide arrangement of the Palearctic species *D. saxonica.* Comparisons of specimens of all castes of the short oculo-malar species from North America with Palearctic specimens of *D. saxonica* demonstrate that they should be assigned to this taxon. The color pattern of all North American *D. saxonica* examined (310 specimens, including 82 queens, 30 males and 198 workers) is usually less extensively yellow than that of most European specimens of that species, but is indistinguishable from melanic Palearctic individuals. The diverse nesting habits exhibited by *D. saxonica* in North America closely correspond to those reported by European workers for Palearctic populations of this species.

In Figure 2, the major mountainous areas of Western North America have been roughly outlined. All of the Nearctic specimens of *D. saxonica* which I have seen have been collected within these areas. East of these mountains only *D. norvegicoides* has been found although this species is also found at lower elevations along the Pacific Coast from the Washington-Oregon border northward to Alaska. Within the distribution of *D. saxonica* limited sympatry of the two species has been noted. The indicated sympatry in Southern Alberta, Canada and in South Central Alaska resulted from collections made by the author. The records from the Mackenzie River Delta came from collections made in 1930 and 1931 by Mr. Owen Bryant. Although the specimens were all labeled Aklavik, N.W.T., specimens of other *Vespula* and *Dolichovespula* species which inhabit very diverse habitats were also identically labeled. In 1976, I went to Inuvik which is about 65 km to the east of Aklavik and also on the Mackenzie River Delta and at the same elevation. At Inuvik, *D. albida* was as common as it is in many other taiga habitats but no other species of yellowjackets were collected. Even now, locations with names are widely separated in the Canadian Arctic and I must suspect that some of the Aklavik specimens may have been collected at considerable distances from the named collecting site, possibly into the Richardson Mountains to the West. Although the author collected *D. albida* in sympatry with *D. saxonica* at Eagle River, AK, the terrain in the MacKenzie River Delta is very dissimilar to any sites where I have collected either *D. saxonica* or *D. norvegicoides* and the Aklavic record of sympatry remains questionable.

The distributional patterns of the two species are less clear at the Northwestern portion of their ranges. It appears that considerable sympatry may occur but it was documented on only one occasion. Although *D. saxonica* inhabits the higher mountain localities in the Canadian Rocky mountains and southward, in Alaska I have only encountered it at lower elevations in association with mixed hardwood/conifer forests. In the taiga and coniferous localities of central and Pacific coastal Alaska, *D. norvegicoides* is quite common. Very few yellowjacket specimens have been available from longitude 150° west

to the Bering Sea due to the relative inaccessibility of that area. Thorough collecting within that area will be essential to the definition of the Northwestern distributional limits of North American species of the *Boreovespula.* Clarification of any interrelationships between Nearctic and Asian faunas will also require similar data from specimen material collected in Eastern Siberia, particularly the Chukotskiy Peninsula.

Key to the North American Dolichovespula

1. Lower half of the sides of the pronotum and lower half of propodeum transversely striate. Moderately large wasps with indistinct dimorphism between queen and worker. Male with two prominent tyloides on the flagellar antennal segments particularly the 6th through the 11th. Black marked with ivory white in the one North American species. The baldfaced hornet, *Dolichovespula maculata* (F.) . . . . . Subgenus *Dolichovespula*

   Lower half of the sides of the pronotum and lower half of propodeum punctate. Smaller wasps with distinct dimorphism between queen and worker. Males with or without tyloides on flagellar antennal segments. Subgenus *Boreovespula* 2

2. Workers not present. Anterior margin of the clypeus in the female with prominent tooth-like lateral angles. Flagellar antennal segments of the males almost entirely black without or with only slight traces of tyloides. Usually marked with ivory-white although in some specimens, particularly from the southwestern United States, the markings are sometimes yellowish. Socially parasitic upon other *Boreovespula* species. . . . . *Dolichovespula arctica* (Rohwer)

   Workers present. Anterior margin of the clypeus in the females with broadly rounded lateral angles. Flagellar antennal segments of males with various arrangements of tyloides 3

3. Pale markings white or ivory-white. Rufous lateral markings usually present on second and sometimes also in the first abdominal tergites in the worker and male. Rufous abdominal marking absent in queen. Ocellar triangle broad; the distance between the posterior pair subequal to their distance from the inner margins of the eyes. A single basal tyloide present on each of the last five antennal segments in the male. . . . . *Dolichovespula albida* (Sladen)

   Pale markings yellow or dirty yellow. Rufous abdominal markings rarely present. Ocellar triangle nearly equilateral; the distance between the posterior pair about 3/4 of their distance to the inner margins of the eyes. Tyloide arrangement different 4

4. Yellow bands of first and second abdominal tergites deeply interrupted by a black median point. Yellow hind margin of pronotum usually produced downward along lateral, vertical carina. Yellow markings along posterior margins of eyes uninterrupted from genal to temporal areas of head. Flagellar antennal segments of the male with two tyloides on each of the apical six segments. Oculo-malar length variable, becoming slightly longer with increasing north latitude . . . . . *Dolichovespula arenaria* (F.)

   Yellow bands of first and second abdominal tergites narrow, continuous, only faintly narrowed medially. Yellow hind margin of pronotum little or not produced downward along the anterior, vertical carina. Yellow markings along posterior margins of eyes usually reduced to spots on the tempora and usually also on the genae 5

5. Oculo-malar length long. Ratio between head width and oculo-malar length less than 6.40 in the worker and 6.20 in the queen. Antennal flagellum of male with two tyloides on each of the apical six segments. Genal markings usually wider than the temporal markings. Yellow bands on abdominal tergites two through five subequal in width. . . . . *Dolichovespula norvegicoides* (Sladen)

   Oculo-malar length short. Ratio between head-width and oculo-malar length greater than 6.40 in the worker and 6.20 in the queen. Antennal flagellum of male with one tyloide on the apical, fifth and sixth segments and two tyloides on the second, third and fourth segments. Genal markings usually narrower than the temporal markings. Yellow bands of increasing width on abdominal tergites two through five, the fifth often bearing a pair of free black spots . . . . *Dolichovespula saxonica* (Fabricius)

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RECENT LITERATURE

Z. Kazab, 1977. Die Tenebrioniden des papuanischen Gebietes I. Strongyliini (Coleoptera, Tenebrionidae Pacific Insects Monograph 33:1-219. 79 figs., 16 plates. Dept. Entomology, Bishop Museum, Honolulu. $10.50 soft cover.

This work treats 169 species in seven genera (four new) of Strongyliini from New Guinea. The work (in German), is formated as are standard taxonomic treatments. The taxa are profusely illustrated (each of the 79 numbered figures contains six to ten or more clear, informative line drawings). The full page plates (black and white) occasionally leave something to be desired, since the darker beetles are so devoid of detail many appear to be hardly more then silhouettes (see pl. VIII, Fig. A; XII, Fig. 1; etc). This would appear to be of a minimal disadvantage, however, in light of the numerous other drawings. Certain to be indespensible to future workers on the group. — ARH.